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BODY TEMPERATURE AND ENERGY METABOLISM OF BROWN LEMMING IN RELA--ETC(U)

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Body temperature and energy metabolism
of brown lemming in relation to running speed

by

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INTRODUCTION

The energetics of microtine rodents are of particular interest because both temperate and arctic microtine rodents of at least four genera exhibit basal metabolic rates significantly greater than predicted based on body mass (Scholander et al, 1950; Hart and Heroux, 1955; Packard, 1968; MacManus, 1974). Several studies of thermoregulation of lemmings have measured metabolism of active animals (Hart and Heroux, 1955; Bashenov, 1968) but there has been as yet no attempt to assess the energetic cost of locomotion in these animals. In view of the close relationship between basal metabolism, metabolic cost of transport, and body mass (Taylor, Rabb and Schmidt-Nielsen 1970) animals having different basal metabolism may also have different activity metabolism.

The present study reports the relation of energy metabolism during locomotion in the brown lemming, Lemmus trimucronatus, as a function of speed, and assesses the importance of heat storage and heat dissipation of lemmings during locomotion.

MATERIALS AND METHODS

The study was performed in July 1978 at the Naval Arctic Research Laboratory, Barrow, Alaska. Brown lemmings were caught locally and maintained in individual rack mounted cages on a diet of Purina rat chow, dog chow, fresh cabbage and fresh carrots.

The treadmill used in this study was a Sears belt sander having a running surface of 14" x 4". A wooden box, filled with foam rubber to reduce the air volume, was built around the treadmill. On the top of the treadmill a sheet of Plexiglas was attached to the wooden box by wing nuts and made airtight with rope caulk. In the center of the Plexiglas sheet a strip 14" x 4" was removed, and a test section 14" x 4" x 4" was inserted and attached with strapping tape. The running chamber contained X inlet and outlet ports and a hinged lid 4" x 4" for inserting and removing the animal. Prior to testing, the seams of the lid were taped with strapping tape.

The treadmill was powered by a 1/6 horsepower motor. Tread-speed was controlled by an E-1 zero-max drive power block (speed range 0-4000rpm) attached directly to the

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sander shaft. Tread speed was calibrated by counting revolutions timed by stopwatch. Due to direct attachment of motor to treadmill, once a given speed was set, it did not vary significantly.

The Lemmings were trained to run at several speeds daily for about a week prior to actual data collection. During the training sessions 2.1 Km/h was determined to be the maximum running velocity which could be sustained for at least 10 minutes. Ten minute experiments were chosen for this study due to a shortage of animals and because a prior study (Hart and Heroux, 1955) indicated that lemmings run for 20 minutes exhibited high mortality due to heat stress.

Air was drawn through an outlet port in the rear of the test chamber at a flow rate of 240 liters/hour. Flowmeters (Matheson 603) were calibrated prior to experiments and checked during the experimental period with a dry test meter. Carbon dioxide production was measured with a Beckman Model 824 Infra-red analyzer (full scale deflection = 0.5% CO₂). The analyzer was calibrated daily using outside air and two primary standard grade gas mixtures of different concentrations. Air was dried prior to analysis by passing it through a cylinder of Drierite (anhydrous calcium sulfate). Output from the analyzer was recorded on a Hewlitt-Packard model 7100B strip chart recorder or taken at 15-30 second intervals from a Fairchild model 7000 digital multimeter. CO₂ (STP) production was converted to heat production assuming glycogen was utilized as fuel (RQ = 1).

Temperature of the air (T_a) flowing through the chamber was measured with a 36 gauge cooper-constantan thermocouple glued to the inside of the outlet port 5 millimeters from the test section. Body temperatures were measured by inserting a polyethylene covered 36 gauge cooper-constantan thermocouple at least 2cm into the rectum. Body temperatures (T_b) were measured immediately prior to and immediately following ten minute experiments. Body temperatures were read to the nearest 0.1°C and ambient temperature to the nearest 0.5°C on a Bailey Instruments laboratory thermometer.

RESULTS

Carbon dioxide production is a linear function of speed between 0.37 and 1.50 Km per hour (fig. 1). The slope of this relation (3.2) is approximately 1.8 times the slope predicted for a 59g rodent based on the regression derived by Taylor et al. (1970). The relation extrapolates to 2.8 ml CO₂ (g · h)⁻¹ at zero running velocity, approximately 1.6 times the resting metabolic rate. At 2.1 Km/h the mean rate of CO₂ production was not significantly different from rates obtained at 1.50 Km/h. These data suggest an aerobic scope for lemmings of at least 6 times BMR.

In most experiments the lemmings ran willing throughout the entire duration. If running was not continuous for at least 10 minutes, the results were discarded. At .75, 1.5 and 2.1 Km/h the level of CO₂ production stabilized within the first two minutes and showed little variability for the remainder of the experiment. At the lowest speed, however, the variability was greater because the animals were not content simply to run but often ran on hind legs while attempting to open the lid with the front legs or attempting to burrow out of the front of the test section. At .37 Km/h, therefore, it was often necessary to run the lemmings for longer than ten minutes to insure a stabilized VCO₂.

Body temperatures increased during running, indicating a portion of heat produced during running was stored in the body rather than dissipated to the environments. Mean body temperature increase was directly related to running speed (table 1). Although VCO₂ did not increase between the speeds of 1.50 and 2.1 Km/h the increased T_b at 2.1 Km/h suggests a higher thermal load at the higher running speed. It is possible that the difference between the predicted VCO₂ based on the regression in figure 1 and measured VCO₂ represents the portion of energy metabolism derived anaerobically. The estimated heat storage necessary to cause the measured increase in body temperature amounts to 22 to 24% of the metabolic heat production.

In a separate series of experiments lemmings were run at 1.5 Km/h for ten minutes inside a constant temperature chamber at T_a = 5°C (the normal mean air temperature

(4)

on the Tundra at Barrow in the summer). Under these conditions body temperatures after running were not significantly different from T_b 's measured before the run (mean temperature change = 0.35, ± 0.2 , N=6).

Discussion

The energy cost of locomotion in lemmings is substantially higher than for other mammals of similar body size. The slope of metabolism vs. speed for lemmings (fig.1) is approximately twice that predicted for a 60 gram mammal based on the regression equation derived by Taylor (1973). Data from the present study are consistent with data obtained by other investigators. Hart and Héroux (1955) obtained a value of $5\text{mlO}_2/\text{g h}$ for collared lemmings (Dicrostonyx groenlandicus) forced to run on a running wheel at 0.54 Km/h ($T_a = 20^\circ\text{C}$), 64% higher than predicted by Taylor et al (1970) and within 10% of the value predicted by my equation. Bashenov (1968) reported a steady-state running metabolism of $7.2 \text{ mlO}_2/\text{g h}$ for lemmings (lemmus obensis) running on a treadmill at 0.9 Km/h at $T_a = 16-18^\circ\text{C}$. This value is approximately 100% higher than metabolism predicted based on Taylor's equation and 26% greater than predicted by equation 1 (Fig 1). As the lemmings were in thermoneutrality at this temperature, elevated energy metabolism does not appear to be due to increased cost for thermoregulation.

The reason for lemmings exhibiting a higher slope of energy metabolism in relation to running speed than other mammals of similar body mass is unclear but it probably is related to mechanical constraints based on their morphology. Lemmings (and other microtine rodents) have spherical bodies and very short legs as compared with mice, rats (suborder cricetidae). In this context Kinematic analysis of stride characteristics of lemmings would be useful in evaluating the degree of mechanical similarity between their locomotion and that of rats, for which good energetic and biomechanical data are presently available (Pedley, 1978). (These experiments are currently underway in my laboratory using a temperate zone microtine rodent, microtus pennsylvanicus).

The intercept of the regression in figure 1 is about 30% higher than predicted (Taylor et al, 1970). This appears to be the result of lemmings having a higher basal

metabolic rate rather than due to constraints for locomotion. Elevated BMR is characteristic of both arctic (Scholander et al, 1950; Hart and Heroux 1955; Coady, 1972; Casey et al, 1979) and temperate zone microtine rodents (MacManus, 1974). The intercept is 1.6 times the basal metabolic rate, and similar results are available for mammals from a wide variety of taxa (see Taylor et al, 1970; Taylor, 1973; for further discussion). The best explanation currently available for the increased metabolism above the resting level is that this increment represents the energy cost of maintaining a running posture (Schmidt-Nielsen, 1972). The present study indicates a similar postural cost in brown lemmings. Since the energy cost above the resting level at zero running speed is a similar proportion as in other mammals there is no reason to assume that a higher basal metabolism has any effect on the energetics of locomotion. This interpretation is consistent with Rabb's (1974) study which demonstrated that the cost of locomotion per se did not differ for nocturnal rodents run day or night despite differences in the level of resting metabolism. Of course, a higher resting metabolism should result in a higher total cost for locomotion at any given speed, but this increase is insignificant and does not explain the difference in slope of the relation from that predicted value.

The capacity of lemmings to thermoregulate during exercise at thermoneutral ambient temperatures is poor judging by the direct relation between T_b and exercise load (table 1). Larger quantities of heat are stored at the higher work outputs (table 1). However, since the fraction of the total heat production which is stored is similar, these data indicate that heat dissipation also increases at higher levels of performance. The most logical source of increased heat exchange is via convection since the animals should be operating at higher limb frequencies while running at high speed, thereby automatically disrupting normal boundary layers and maximizing surface areas available for heat dissipation.

A further avenue of heat exchange which may vary at different activity levels is

respiratory evaporation, as a direct consequence of the higher ventilation volumes which necessarily follow from increased O_2 demand during running at high speed. However, in view of the high rates of oxygen consumption of the lemmings under these conditions, it is quite unlikely that their ventilation is controlled for anything but oxygen transport, making respiratory evaporation merely a passive factor related to metabolic rate and movement of air through the lungs rather than a factor which can be regulated to control T_b . This interpretation is consistent with that of Rabb and Schmidt-Nielsen (1974) who demonstrated that evaporative water loss was responsible for only a small fraction of the heat dissipated by Kangaroo rats and also that it was not regulated by the animal.

Previous studies of lemmings forced to run at a single speed at several different ambient temperatures also suggest a poor capacity for thermoregulation during activity (Hart and Heroux, 1955; Bashenov, 1968). Although insulation of the animals during activity was reduced, facilitating dissipation of endogenous heat production, body temperature declined at low T_a ($< 0^\circ C$) indicating that heat loss exceeded heat production, while the reverse was true at "high" $T_a (> 10^\circ C)$. Several collared lemmings died apparently of heat prostration when forced to run at 0.54 Km/hr for 20 minutes at T_a 's greater than $20^\circ C$ (Hart and Heroux, 1955). In the present study, although animals ran for 10 minutes at speeds up to four times faster, heat prostration did not appear to be a significant problem. However, my animals were in summer pelage. If Hart and Heroux's animals were in winter pelage, this would greatly reduce the ability to dissipate heat. The fact that lemmings in the present study did not develop hyperthermia when forced to run at high speed under natural ambient temperatures suggests that the degree of insulation provided by their summer pelage is optimal for allowing thermoregulation during activity.

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Table 1. Body temperature, heat production and heat storage in relation to running speed. Numbers in parentheses at 2.07 Km include estimated heat produced anaerobically.

Running speed (Km/h)	ΔT_b	Heat production (Joules)	Heat stored (Joules)	% of HP stored
0.75	1.18	1076	238	22
1.50	1.84	1561	372	24
2.07	2.33	1587	473	30.4
		(1972)		(24)

Figure Legend

Fig. 1. Carbon dioxide production (mean \pm standard deviation) of brown lemmings in relation to running speed. Numbers indicate sample size. Linear regression for data at the three slowest speeds.



